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**The *Beothukis/Culmofrons* problem and its bearing on Ediacaran  
macrofossil taxonomy: evidence from an exceptional new fossil  
locality**

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**Abstract:** The late Ediacaran siliciclastic successions of eastern Newfoundland, Canada, are renowned for their fossils of soft-bodied macro-organisms, which may include some of the earliest animals. Despite the potential importance of such fossils for evolutionary understanding, the taxonomic framework within which Ediacaran macrofossils are described is not clearly defined. Rangeomorphs from a newly discovered fossil surface on the Bonavista Peninsula, Newfoundland, require us to reconsider contemporary use of morphological characters to distinguish between genera and species within Ediacaran taxa. The new surface exhibits remarkable preservational fidelity, resolving features smaller than 0.1mm in dimension in both frondose and non-frondose taxa. Such preservation permits the recognition of rarely-observed fourth- and fifth-order rangeomorph branching, offering

unparalleled opportunities to investigate the fine-scale construction of rangeomorph taxa including *Culmofrons plumosa* Laflamme *et al.*, 2012. Our observations enable resolution of taxonomic issues relating to rangeomorphs, specifically overlap between the diagnoses of the frondose genera *Beothukis* Brasier and Antcliffe, 2009 and *Culmofrons*. We propose a taxonomic framework for all Ediacaran macrofossils whereby gross architecture, the presence/absence of discrete morphological characters, and consideration of growth program are used to distinguish genera, whereas morphometric or continuous characters define taxa at the species-level. On the basis of its morphological characters, *Culmofrons plumosa* is herein synonymized to a species (*Beothukis plumosa* comb. nov.) within the genus *Beothukis*. This discussion emphasizes the need to standardize the taxonomic approach used to describe Ediacaran macrofossil taxa at both the genus and species level, and raises important considerations for future formulation of higher-level taxonomic groups.

**Key words:** Rangeomorph, Ediacaran, Newfoundland, systematics

THE late Ediacaran strata of Newfoundland record some of the oldest fossil evidence for large, soft-bodied organisms. Fossils are typically preserved beneath volcanic tuffs or volcanoclastic sediments, deposited in deep-marine turbiditic environments (Wood *et al.* 2003; Ichaso *et al.* 2007; Brasier *et al.* 2013; Mason *et al.* 2013) ~580–560 Ma (Benus 1988; Van Kranendonk *et al.* 2008). The Newfoundland biota includes many taxa whose biological affinities have been widely debated (summarised in Liu *et al.* 2015). In recent years, researchers have tended to interpret Ediacaran macrofossils on a case-by-case basis, proposing that a range of biological groups, including bacteria (Callow and Brasier 2009a; Laflamme *et al.* 2011), and potentially algae (Hofmann *et al.* 2008), fungi (Callow and

Brasier 2009b), and metazoans (Liu *et al.* 2014a; Liu *et al.* 2014b), co-existed in the Ediacaran marine ecosystems of Newfoundland.

The most abundant and diverse macroscopic group within the Newfoundland successions is the Rangeomorpha (Liu *et al.* 2015), members of which are characterised by the possession of self-similar branching architectures (Narbonne 2004; Brasier *et al.* 2012). The preservation of rangeomorphs in the manner typical of Avalonian (eastern Newfoundland and the southern UK) Ediacaran macrofossils, on siliciclastic bedding planes as external molds and casts (cf. Kenchington and Wilby 2014), contributes to a dearth of diagnostic morphological characters with which to constrain their phylogenetic affinities.

There is no clear and consistent taxonomic framework within which to describe Ediacaran macrofossils, many of which are not currently attributable to living clades. Efforts have been made to formulate high-level schemes by grouping genera within higher-order Linnaean ranks (e.g. Sepkoski in Schopf and Klein 1992) or non-Linnaean groupings (Laflamme *et al.* 2013; Grazhdankin 2014). A robust taxonomic framework is important, since the genera and species that form the basis of existing Ediacaran groups have been employed as the foundation both for efforts to determine relationships between taxa, and for discussions of palaeoecological attributes such as diversity, disparity, and population structure (e.g. Clapham *et al.* 2003; Darroch *et al.* 2013). Despite this, there has been little agreement or even discussion of the characters or features that might usefully define Ediacaran genera with respect to species. If we are to make effective progress in Ediacaran palaeobiology, the formulation of generally accepted taxonomic protocols is imperative. This attractive proposition is impeded by the need to consider non-uniformitarian and often abiological interpretations for many preserved structures (e.g. Brasier *et al.* 2013), and by preconceptions of the possible physiology of Ediacaran organisms—necessarily guided primarily by extant taxa— which may introduce artificial biases to taxonomic schemes.

However, the greatest limitation to our understanding of the morphological construction and ontogeny of the Ediacaran macrobiota is often the quality of the available fossil record.

Much of the progress made in Avalonian Ediacaran palaeobiology stems from data collected at a handful of localities exhibiting high-quality macrofossil preservation (e.g. the ‘D’ and ‘E’ Surfaces of the Mistaken Point Ecological Reserve, or the bedding plane at Spaniard’s Bay; Clapham *et al.* 2003; Narbonne 2004). Recent discoveries have significantly increased the number of known fossil-bearing sites, most notably on the Bonavista Peninsula (O'Brien and King 2004; Hofmann *et al.* 2008), and in Charnwood Forest in the United Kingdom (Wilby *et al.* 2011). A bedding plane on the east coast of Burnt Point, near the town of Port Union, Bonavista Peninsula, formally documented here for the first time (Fig. 1), is remarkable for its high-quality preservation of Ediacaran macrofossils. The horizon exhibits high taxonomic diversity, and a wide size-range of taxa including some of the largest and smallest rangeomorphs yet discovered. The surface is named the MUN Surface to reflect the long history of research on Newfoundland’s Ediacaran successions by researchers from the Memorial University of Newfoundland (MUN). Importantly, preservational fidelity on the MUN Surface permits assessment of the architectural scheme of Brasier *et al.* (2012) in defining rangeomorph taxa. Here we use MUN Surface specimens to; assess the role morphological characters (including those not relating to branching architecture) can play in rangeomorph systematics; resolve a taxonomic conundrum relating to the genera *Beothukis* and *Culmofrons*, and; propose an extension of the classification approach of Brasier *et al.* (2012) for rangeomorphs to other Ediacaran macrofossil groups. We also consider some of the broader issues surrounding incorporation of Ediacaran taxa into higher-level taxonomic groups, which may aid future development of a consistent global higher-rank taxonomic scheme for these perplexing organisms.

## THE MUN SURFACE FOSSIL ASSEMBLAGE

The MUN Surface lies near the base of the Port Union Member of the Trepassey Formation (cf. O'Brien and King 2005; Fig. 1), within an interval dominated by medium- to thick-bedded buff-grey turbiditic sandstones with soft-sediment deformation, rounded intraclasts, and centimetre- to decimetre-scale carbonate concretions (Supp. Figs 1–2; Supp. Text 1). Fossils are preserved as positive and negative epirelief impressions on a siltstone surface, beneath a ~6 mm-thick fine-grained tuff layer (Supp. Fig. 3), which is itself overlain by 3–20 cm-thick beds of grey to grey-green siltstone and coarse sandstones (Supp. Figs 1–2).

Fossils on the MUN Surface occur in densities of up to 45 well-preserved individuals/m<sup>2</sup>, with over 250 exceptionally preserved identifiable specimens on a total exposed surface (at low tide) of ~120m<sup>2</sup> (Figs 2–3, Supp. Fig. 4). Around 500 small, indistinct impressions not included in this biotic density count represent additional poorly preserved juvenile specimens (e.g. Supp. Fig. 4). The most striking fossils are members of the Rangeomorpha (Narbonne 2004; Laflamme *et al.* 2013), and include: at least 40 specimens of a unipolar form (i.e. possessing a single apical generative zone) comparable to *Culmofrons plumosa* (Fig. 2A; Supp. Fig. 6; see later discussion); seven large specimens of *Bradgatia* aff. *linfordensis* Boynton and Ford, 1995 (Fig. 2B–C); 43 *Primocandelabrum* sp. Hofmann *et al.*, 2008 (Fig. 3A); rare *Fractofusus andersoni* Gehling and Narbonne, 2007 (Fig. 3C); and *Charnia masoni* Ford, 1958 (Fig. 3D). Other taxa include numerous *Charniodiscus* spp. including *C. procerus* Laflamme *et al.*, 2004 (Fig. 3B); isolated holdfast discs; a single partial specimen of the possible cnidarian *Haootia quadriformis* (Liu *et al.* 2014a, fig. 1f); *Thectardis avalonensis* Clapham *et al.*, 2004; four *Hadryniscala avalonica* Hofmann *et al.*, 2008; and several poorly defined ivesheadiomorphs (cf. Liu *et al.* 2011). Specimens range in size from 10 mm to 0.7 m in maximum dimension, and can preserve features ~0.1 mm in dimension (Fig. 2C), a quality of morphological resolution comparable to that of the younger

Ediacara Hills (South Australia) and White Sea (Russia) assemblages (e.g. Gehling and Droser 2013). Some rangeomorph specimens exhibit up to five orders of self-similar branching (e.g. Fig. 2C; Supp. Fig. 5), whereas other notable fossil surfaces in Newfoundland typically preserve only two or three. In addition to taxa assignable to known late Ediacaran genera, a dense fabric of 100s of thin filamentous impressions is also present (Fig. 3E). Filamentous structures are arranged in multiple orientations on the bedding plane, and can both drape and underlie macrofossil taxa. Individual filaments are 0.2–0.6 mm in width, but can reach up to 400 mm in length. They exhibit no internal or external ornament, and show no clear branching.

A tectonic overprint is evident on the surface, both as two sets of cleavage fractures oriented at 016° and 350° respectively, and as deformation of holdfast discs (assumed from study of multiple specimens to have originally been circular) to oval shapes. The holdfast discs have an aspect ratio (width/length) of 0.73 (mean value taken from 20 specimens to 2 d.p., relative standard deviation 6.35%), with long axes oriented along a NNE-SSW axis (i.e. broadly along strike), consistent with regional compressive tectonism associated with the formation of the Catalina Dome.

## **THE TAXONOMY OF EDIACARAN RANGEOMORPHS**

Taxonomy forms the framework for many current and previous attempts to understand Ediacaran organisms and their palaeoecology. However, there are no clear definitions of what constitutes a species-level characteristic as opposed to a generic attribute within Ediacaran macrofossil taxonomy, let alone agreement on a framework for the higher-order classification of these taxa. Until we have a better handle on their biological affinities, it is difficult to be sure about how fixed the phenotype of these organisms was, and the extent to which they

conform to the morphological and biological species concepts. We consider that as understanding of Ediacaran palaeobiology and palaeoecology improves and attention turns to global questions, a standardized, consistently applied scheme for the diagnosis of Ediacaran macrofossil taxa would be advantageous. Here, we address the characters used to define Ediacaran rangeomorphs in light of the new MUN Surface specimens.

The broad concepts of what constitutes a genus, and how genera should be objectively defined, have been long debated (e.g. Calman 1949; Mayr 1963; Melville 1995). Calman (1949, p. 17) notes that the genus “*has no objective existence as a group but is merely a convenient device to make easier the cataloguing and handling of numbers of species*”. Calman further proposed that in establishing new genera, distinguishing characters “*should be such as we may reasonably suppose [them] to be longer established in phylogeny than those distinctive of species*” ... remaining “*unchanged amid variations in other characters*” when assessing a group of related forms (Calman 1949, p. 17).

Late Ediacaran fossil assemblages commonly offer only small populations of specimens, of variable preservational quality. Assessment of the variability of characters within populations can therefore be difficult. In recent years, increased awareness and understanding of wider global sections and sedimentological and taphonomic processes has resulted in considerable taxonomic synonymization (see Fedonkin *et al.* 2007). Amongst Avalonian taxa, discoidal forms have largely been synonymized (e.g. Gehling *et al.* 2000), but there has also been much work to formally describe new non-discoidal taxa. Most existing Avalonian Ediacaran genera are monospecific (see Liu *et al.* 2015, table 1). Since rangeomorphs are common in Newfoundland, and are one of the few groups with a widely recognized shared morphological attribute (the possession of self-similar branching within cm-scale specimens; Narbonne 2004; Brasier *et al.* 2012; Hoyal Cuthill and Conway Morris 2014), they offer a useful case study for Ediacaran taxonomic questions.



Many Ediacaran macro-organisms are preserved only as mould or cast impressions on rock surfaces, so when discussing their taxonomy we are exclusively dealing with morphotypes. Macrofossil taxa in Newfoundland were originally distinguished by the presence or absence of characters such as central rods and stems/stalks, and by variations in gross shape, branch shape, branching angle, number of branches, and polarity (e.g. Hofmann *et al.* 2008; Bamforth and Narbonne 2009; Narbonne *et al.* 2009; Laflamme *et al.* 2012). However, some of these parameters, such as branch angle and number of branches, have since been recognised to vary within populations of certain species, for example through ontogeny (e.g. Liu *et al.* 2012), and have therefore been suggested to be unsuitable for use in taxonomic diagnosis (Wilby *et al.* 2015). There has also been little consistency in whether formal diagnoses have been assigned to the genus (as with *Beothukis*, *Pectinifrons*, *Primocandelabrum*, *Parviscopa*, *Hapsidophyllas*, *Fronidophyllas*, *Vinlandia*), or the species (e.g. *Avalofractus*, *Culmofrons*), in monospecific taxa. Diagnosing the species within a monospecific genus would prevent creation of further species within that genus, so we urge future workers to only diagnose species when multiple species exist within a genus. More enlightening in terms of addressing taxonomic methodologies are taxa with multiple species, such as *Fractofusus* or the arboreomorph *Charniodiscus*, in which gross morphology defines the genus, and variations in frond shape, number of branches, length-width ratios and the presence/absence of subsidiary branches have been considered to be species-level traits (cf. Laflamme *et al.* 2004; Gehling and Narbonne 2007). More recently, the structural architecture of rangeomorph branches has been considered a valid characteristic with which to discriminate between rangeomorph taxa, leading to the formalization of a taxonomic scheme based on branching architecture (Narbonne *et al.* 2009; Brasier *et al.* 2012). This scheme is largely consistent with existing rangeomorph taxonomy, and proposes that the presence or absence of structural features such as holdfast discs, and branching architecture

(the way in which branches are arranged within a frond), are genus-level traits, whereas morphometric or continuous characters (such as number of branches and shape of the frond) would either be better suited for the diagnosis of species, or used only with caution as diagnostic criteria, since they may have been subject to ecological or ontogenetic influences (Brasier *et al.* 2012).

The MUN Surface specimens conform to the concepts of branch furling, display, and inflation proposed as suitable characters for taxonomic identification within the rangeomorphs (Brasier *et al.* 2012). They may also permit future extension of such concepts to consider variation in branching morphologies within 3<sup>rd</sup>–5<sup>th</sup> order sub-units. Exceptionally preserved MUN Surface specimens of unipolar forms similar to *Culmofrons plumosa* warrant further attention, since they lie at the heart of a conundrum that has a bearing on how rangeomorphs are diagnosed.

*The genera Beothukis and Culmofrons.*

*Culmofrons plumosa* was formally described in March 2012 (Laflamme *et al.* 2012), at a similar time to the publication of Brasier *et al.* (September 2012) in which morphological architecture was suggested as a means of characterising rangeomorph taxonomic diagnoses.

The genus *Culmofrons* was erected using material from the Mistaken Point region of the Avalon Peninsula (Laflamme *et al.* 2012). *Culmofrons plumosa*, the type species, was diagnosed as follows (note that the generic diagnosis of *Culmofrons* is “as for species”):  
“Rangeomorph frond with a spatulate to ovate petaloid composed of few (less than five on each side) alternating primary branches forming a zigzagging central axis. Basal primary branches attach directly to a long cylindrical stem and circular unornamented holdfast. Primary branches composed of several (between 8 to 12) sub-rectangular to trapezoidal

secondary modular units oriented perpendicularly to the primary branches. Secondary modular units composed of cm-scale rangeomorph frondlets” (Laflamme *et al.* 2012, p. 195).

It is clear from this description, and from images of the type material (Fig. 4C; Laflamme *et al.* 2012), that some of the best-preserved rangeomorph fossils on the MUN Surface are encapsulated by the diagnosis of *C. plumosa* (e.g. Figs 2A, 4B). However, some of these MUN Surface specimens were figured as part of the emended diagnosis of the rangeomorph genus *Beothukis* (Brasier *et al.* 2012, fig. 8B), and provide the basis for the following emended generic diagnosis of *Beothukis*:

“Frond unipolar, comprising two rows of primary branches arranged in irregularly spaced alternations along a furled central axis, forming a linear suture. Inflation of first- and second-order branches is moderate to medial. Mature first- and second-order branches typically have furled margins, with alignments that are arranged in radiating to subparallel series. Rangeomorph elements of the first-order branches are usually undisplayed, whereas those of second-order branches are clearly displayed. A basal disc and stem is sometimes preserved” (Brasier *et al.* 2012, p. 1114).

As with the diagnosis of *Culmofrons*, it is clear that the MUN Surface material could equally be assigned to the genus *Beothukis* as defined by Brasier *et al.* (2012), though our new material differs in possessing a zigzag rather than a linear central axis. We are thus faced with a taxonomic conundrum that requires resolution.

Following the Brasier *et al.* (2012) scheme for classifying rangeomorph genera, focusing solely on branching architecture, requires that the MUN Surface specimens be assigned to *Beothukis*, which has taxonomic priority. However, as stated by Laflamme *et al.* (2012), there are several clear differences between the type material of *Beothukis mistakensis* Brasier and Antcliff, 2009 (currently the sole species of *Beothukis*), and *Culmofrons*; namely the presence in the latter of a long stem, fewer than five primary branches, and a

zigzag central axis (see Table 1; Laflamme *et al.* 2012, p. 197–198; Fig. 4D), and these differences are shared by our specimens (Fig. 4; Supp. Fig. 6). It is therefore imperative to consider whether the morphological details in which these taxa differ reflect species or genus-level characters. Throughout this discussion, we suggest that the taxonomic importance ultimately ascribed to a character is dependent on whether its morphological appearance in an organism is considered to be the result of inherent genetically-based programming, or extrinsic factors in the palaeoenvironment.

The course of the midline (straight or zig-zag) is a weak taxonomic character in rangeomorphs since it may be prone to taphonomic variability (Laflamme *et al.* 2007; Brasier *et al.* 2012). In contrast, the presence or absence of a basal disc is considered a key character in the Brasier *et al.* framework, and this line of reasoning could be extended to the presence or absence of a stem. The original diagnosis and description of *Beothukis* (Brasier and Antcliffe 2009) do not mention a stem or a holdfast disc, but the diagnosis was emended by Brasier *et al.* (2012) to state that a “*stem is sometimes preserved*” (2012, p. 1114). Importantly, the emended specific diagnosis of *B. mistakensis* by Narbonne *et al.* (2009) notes that although a stem is typically not present, it can be observed, and is <5% of the length of the frond when present. It therefore appears that although a stem is not frequently seen in *Beothukis mistakensis* (perhaps due to taphonomic reasons), it is present in some specimens. Specimens previously assigned to the genus *Culmofrons* (cf. Laflamme *et al.* 2012) possess a stem that comprises 29–42% of the length of the organism (values calculated using data presented in Laflamme *et al.* 2012, table 1), demonstrating that considerable variability in stem length is observed within what has previously been considered to be a single taxon. Given these discussions, it appears that *Culmofrons* and *Beothukis* specimens as previously defined differ not in the presence of a stem, but in its length. The presence/absence of a stem is a key morphological attribute of undoubted value to the organism, but we

consider that taxonomic diagnoses should not be based on the inferred ecological function of a morphological characteristic (cf. Laflamme *et al.* 2012) until we can be assured that the character in question represents genetic (as opposed to ontogenetic, taphonomic or ecophenotypic) variability. Since stem length in *Culmofrons* does show variation within populations and is seemingly unlinked to other morphological differences, until further evidence can be presented to the contrary, we consider it appropriate to suggest that stem length in that taxon is likely to be an ecophenotypic trait rather than a genetic one. The length of a stem (relative to total length or frond length) could be regarded as a continuous character. We therefore do not consider stem length as a means to distinguish between closely related taxa at the level of genus.

The number of primary branches in rangeomorphs has previously been suggested to be a character that should only be used with caution in their taxonomy (Brasier *et al.* 2012; Wilby *et al.* 2015), since in some taxa it has been demonstrated to vary during ontogeny (e.g. *Charnia* in Antcliffe and Brasier 2007; Liu *et al.* 2012). The number of branches is arguably a continuous character, and therefore we argue that it should only be used as a species- or population-level trait. The suggestion that some taxa have an upper limit on the number of primary branches they possess (e.g. *Culmofrons*), while others seemingly appear to add branches indefinitely (e.g. *Charnia*, Liu *et al.* 2012; Wilby *et al.* 2015), may indicate a substantially different growth program that arguably transcends species-level distinction. Capping the number of primary branches produces a growth plan in *Culmofrons* (Fig. 4C) that—in mature specimens—is entirely dependent on inflation of primary branches and addition only of higher-order (e.g. secondary) branches for growth. In contrast, *B. mistakensis* can have as many as ten primary branches per row (Laflamme *et al.* 2012). Both of these growth plans are compatible with an overall indeterminate mode of growth whereby the organisms continue to grow indefinitely (as seen in other rangeomorphs such as *Charnia*;

Wilby *et al.* 2015). Current data suggest that *Culmofrons* had a finite limit on the number of primary branches, whereas *B. mistakensis* did not. This strongly supports distinction of these taxa at a higher taxonomic level than the species. However, we note that few large specimens of *B. mistakensis* have been described, which importantly means we cannot yet be sure that *B. mistakensis* did not also cap its branch addition, but at a later stage in its developmental program. As it is currently not possible to refute this possibility, we suggest that it would be unwise to separate these taxa on the basis of assumed differences in growth strategy until further evidence is available.

In summary, our assessment of figured material of both *Culmofrons* and *Beothukis* specimens, and material from the MUN Surface, leads us to conclude that differences between these taxa in the linearity of the frond midline and the length of the stem are either continuous variables, or subject to taphonomic influence. Although we also consider the total number of primary branches to be a continuous variable, we recognise that the apparent presence of a discrete cap to the number of primary branches in *Culmofrons* may reflect a significantly different growth program to that seen in *Beothukis*, where branches appear to be added continuously throughout growth. If this is demonstrated to be the case in the future, we would consider such a difference in growth program to be a character of taxonomic significance above the species level. However, given the paucity of large (>25cm) specimens of *B. mistakensis*, we cannot currently refute the possibility that *B. mistakensis* also limits branch addition at a later stage in its growth cycle. We therefore suggest that these organisms can currently be shown to differ only in characters we consider to reflect variation at a species level. We recommend that these taxa are grouped within the same genus, and since *Beothukis* has taxonomic priority, we suggest inclusion of *Culmofrons plumosa* within the genus *Beothukis* to create *Beothukis plumosa* comb. nov. The relevant specimens we describe from the MUN Surface (e.g. Figs 2A, 4B; Supp. Fig. 6; Brasier *et al.* 2012, fig. 8B) are

hereby assigned to the newly described *B. plumosa* comb. nov. The emended diagnosis of Brasier *et al.* (2012) for the genus *Beothukis* requires minor changes to the discussion of stems (see below). We also provide emended diagnoses for the species *B. mistakensis* and *B. plumosa* comb. nov. to consider their branch architecture, and the importance of the morphological differences between them.

## SYSTEMATIC PALAEOONTOLOGY

### Genus BEOTHUKIS Brasier and Antcliffe, 2009

*Type species. Beothukis mistakensis* Brasier and Antcliffe, 2009, from the late Ediacaran of the Mistaken Point Ecological Reserve, Newfoundland, Canada.

*Emended diagnosis.* Frond unipolar, comprising two rows of primary branches arranged in irregularly spaced alternations along a furled central axis. Inflation of first- and second-order branches is moderate to medial. Mature first- and second-order branches typically have furled margins, with alignments that are arranged in radiating to sub-parallel series. Rangeomorph elements of the first-order branches are undisplayed, whereas those of second-order branches are clearly displayed. A basal disc and stem can be present.

### *Beothukis mistakensis* Brasier and Antcliffe, 2009

#### Figure 4A

- 1991 *Rangea* sp.; Gehling, pl. 3.1.  
1992 “Flat recliner”; Seilacher, p. 608–609, fig. 1 (*partim*, bottom row, third from right), fig. 2 (*partim*, upper left).  
1992 “Folding over”; Seilacher, p. 609, fig. 3 (*partim*, top right).  
1999 “other form”; Seilacher, p. 98, fig. 3 (*partim*, lower right of fossil block sketches).

346 2001 “Small tree-like form” and “*Charnia* composite morph”; Narbonne, Dalrymple and  
 347 Gehling, p. 26, pl. 1E and H (*partim*).  
 348 *non* 2003 “small, unnamed frond-shaped fossil”; Wood, Dalrymple, Narbonne, Gehling and  
 349 Clapham, p. 1383, fig. 9.  
 350 2004 Unnamed frond; Laflamme, Narbonne and Anderson, p. 830, fig. 3.1 (*partim*).  
 351 2004 “short-stemmed rangeomorph frond”; Narbonne, p. 1143, fig. 3B–C.  
 352 2004 “Bush-like form”; O’Brien and King, p. 207–210, fig. 3f, pl. 5a.  
 353 2005 “Spatulate rangid” and “short stem rangid”; Narbonne, Dalrymple, Laflamme, Gehling  
 354 and Boyce, p. 28, pl. 1K and 1N.  
 355 2007 “Rangeomorph fronds”; Ichaso, Dalrymple and Narbonne, p. 28, fig. 3C–D.  
 356 2008 “*Charnia antecedens*”; Hofmann, O’Brien and King, p. 17, fig. 13.7 (*pars*), (*non* figs  
 357 13.8 – 13.10, 15.1–15.5).  
 358 2008a “Rangeomorph frond”; Laflamme and Narbonne, p. 184, fig. 2.5.  
 359 2008b “Spatulate rangeomorph”; Laflamme and Narbonne, p. 170, figs 4.4, 4.6, 4.7.  
 360 2009 *Beothukis mistakensis*; Brasier and Antcliffe, p. 382–383, figs 17a–b, 18a–b.  
 361 2009 *Beothukis mistakensis*; Narbonne, Laflamme, Greentree and Trusler, p. 508–514, figs  
 362 3.3 (*partim*), 3.6 (*partim*), 5.1–5.2, 6.1–6.7, 7, 8.1–8.6.  
 363 2012 *Beothukis mistakensis*; Dornbos, Clapham, Fraiser and Laflamme, p. 58, fig. 5.2c.  
 364 2012 *Beothukis mistakensis*; Brasier, Antcliffe and Liu, p. 1116, fig. 5C–D.  
 365 2013 *Beothukis* sp.; Brasier, Liu, Menon, Matthews, McIlroy and Wacey, p. 130, figs 9D,  
 366 11B–D.  
 367 2013 *Beothukis*; Darroch, Laflamme and Clapham, p. 596, fig. 2B.  
 368 2013 *Beothukis mistakensis*; Laflamme, Darroch, Tweedt, Peterson and Erwin, p. 562, fig.  
 369 2.1–2.4.



2013 *Beothukis*; Macdonald, Strauss, Sperling, Halverson, Narbonne, Johnston, Kunzmann,  
 Schrag and Higgins, p. 257, fig. 6C.

2014 *Beothukis mistakensis*; Xiao, p. R121, fig. 1b. [cop. Narbonne *et al.* 2009, fig. 7].

2014 *Beothukis mistakensis*; Hoyal Cuthill and Conway Morris, p. 13123, fig. 1.

2014 *Beothukis*; Ghisalberti, Gold, Laflamme, Clapham, Narbonne, Summons, Johnston and  
 Jacobs, p. 2, fig. 1e (*partim*, lower right).

2014 *Beothukis* cf. *Beothukis mistakensis*; Narbonne, Laflamme, Trusler, Dalrymple and  
 Greentree, p. 215, fig. 6.1–6.7.

2014 *Beothukis*; Zalasiewicz and Williams, p. 144, fig. 13.

2015 *Beothukis mistakensis*; Liu, Kenchington and Mitchell, p. 1361, fig. 2B.

2015 *Beothukis*; Burzynski and Narbonne, p. 37, figs 4a (*partim*, upper left), 5B(b).

*Emended diagnosis.* Frond unipolar and spatulate to ovate in shape, comprising two rows of  
 five or more primary branches (in specimens of > 2cm in length; juveniles may have fewer)  
 arranged alternately along a furled, broadly linear central axis. First- and second-order  
 branches typically exhibit furled margins, and moderate to medial inflation. Second-order  
 branches are arranged in a radial to sub-parallel arrangement. A circular basal holdfast disc  
 and a short stem are sometimes present, but the length of the stem is typically <5% of the  
 length of the frond when observed.

*Beothukis plumosa* comb. nov.

Figures 2A, 4B–C; Supp. Fig. 6A–J, L(*partim.*), N–P.

2007 “Frond”; Laflamme, Narbonne, Greentree and Anderson, p. 249, fig. 6d–e.

v\* 2012 *Culmofrons plumosa*; Laflamme, Flude and Narbonne, p. 196, figs 2.1–2.4, 2.7 (*non* figs 2.5–2.6).

v. 2012 “*Beothukis* sp.”; Brasier, Antcliffe and Liu, p. 1120, fig. 8b.

2014 *Culmofrons*; Kenchington and Wilby, p. 105, fig. 2a [cop. Brasier *et al.* 2012].

2015 *Culmofrons plumosa*; Liu, Kenchington and Mitchell, p. 1361, fig. 2e.

*Diagnosis.* Frond unipolar and spatulate to ovate in shape, comprising two rows of primary branches (with fewer than five branches in each row) arranged alternately along a furled, often zigzagging central axis. Second-order branches (typically 8–12 per first-order branch, but reducing in number distally) are arranged in a broadly sub-parallel to radiating arrangement. A circular basal holdfast disc and a long cylindrical stem (comprising ~30–40% of the length of the organism) are present. A broad, smooth region is often present at the junction between frond and stem.

*Discussion.* We note that for the specific case of distinguishing juvenile *B. mistakensis* with relatively few branches from juvenile *B. plumosa* comb. nov., if a clear stem is not evident or the specimen is poorly preserved, it may be advisable to use open nomenclature (*Beothukis* sp.).

## **EXTENSION OF AN ARCHITECTURAL APPROACH TO WIDER EDIACARAN TAXONOMY**

The discussion above builds upon the use of branching architecture and the presence or absence of key discrete morphological features as generic characters in rangeomorphs, with morphometric or continuous variables used to discriminate between species. Extension of a

similar approach to other Ediacaran taxa would be valuable, as would a search for further potential synapomorphies with which to group possible higher-level clades. The most comparable group to consider is the arboreomorph/frondomorph clade (cf. Laflamme *et al.* 2013; Grazhdankin 2014), many members of which bear superficial morphological similarities to the rangeomorphs. A lack of rangeomorph elements in arboreomorphs precludes use of the exact terms used by Brasier *et al.* (2012), but detailed study of their architecture may yet reveal comparable variability in branch construction (cf. Laflamme and Narbonne 2008b). The use of branch architecture and presence/absence of stems and holdfasts (i.e. discrete characters) as genus-level characters in the Arboreomorpha, with morphometric differences (i.e. continuous characters) being species-level discriminating characters, should be straight-forward. This approach is broadly consistent with existing *Charniodiscus* taxonomy based on material from Newfoundland (Laflamme *et al.* 2004; Laflamme and Narbonne 2008b).

Extension of an architectural approach to non-frondose taxa requires consideration of alternative independent characters that can undergo morphometric or continuous variation. Symmetry has been suggested as a basis for higher order taxonomy (Fedonkin 1985; Erwin *et al.* 2011; Laflamme *et al.* 2013), but more subtle characters are required for fine-tuning at the generic and species levels. The concepts of polarity, rows, and inflation (cf. Brasier *et al.* 2012) could equally be applied to the ‘pneus’ or ‘segments’ of taxa such as *Dickinsonia* or *Pteridinium*, but other groups such as tubular body fossils (e.g. *Wutubus*; Chen *et al.* 2014), may require inspection of additional features, such as branching style, consistency of width, or segment cross-sectional profile.

Difference in growth program between taxa solely growing by inflation, or by both addition and inflation of branches or segments can potentially be of use in distinguishing taxa at the generic or higher levels. However, such distinction should only be accepted if the

perceived difference in growth program can be clearly demonstrated, and is not simply a later change in a growth plan common to both taxa (e.g. the limiting of primary branches at eight branches rather than four). Morphological characters used for taxonomic purposes must be clearly independent of ecological, taphonomic and ontogenetic variation.

The rationale for grouping Ediacaran macrofossils into higher clades, a topic that has long attracted discussion (e.g. Fedonkin 1985) also requires consideration. Two recent studies have resulted in broadly similar schemes that jointly recognize some groups (e.g. the Rangeomorpha), but differ in suggesting distinct names and characteristic features for some groups (e.g. Arboreomorpha vs. Frondomorpha), or including different taxa within similar overall groups (e.g. the Dickinsoniomorpha; Laflamme *et al.* 2013; Grazhdankin 2014). Both studies take a phenetic approach to classification, with Laflamme *et al.* (2013) explicitly using unique synapomorphies to recognize clades whenever possible. However, both studies also propose groupings diagnosed by non-unique characters or character combinations. For example, the Frondomorpha of Grazhdankin (2014, p. 271–272) are described as taxa “composed of a large, relatively flattened foliate section, a central stem, and a holdfast or rooting anchor”; a description that could be used to describe several rangeomorphs (e.g. *Trepassia* or *Beothukis*). Similarly, the suggestion that members of the Arboreomorpha possess primary branches that “end at an outer margin” (Laflamme *et al.* 2013, following Erwin *et al.* 2011 supplementary information) would lead to the inclusion of rangeomorph specimens such as *Beothukis plumosa* comb. nov. from the MUN Surface (Fig. 4B) within that group. We should perhaps not expect all authors to converge on the same higher-order groupings for Ediacaran taxa, and the debate promoted by the differences their schemes reveal is welcomed. However, the characters by which those groups are distinguished should, where possible, be chosen such that they are unique to the proposed clade, potentially paving the way for future application of phylogenetic approaches to these fossils. Adoption of a

‘bottom up’ approach to Ediacaran macrofossil taxonomy—first reaching agreement on methods to distinguish genera and species before progressing to higher levels—seems an appropriate course of action.

## CONCLUSIONS

It is hoped that refinement of Ediacaran morphological and taxonomic studies will lead to wider appreciation of the similarities and differences between Ediacaran macrofossil taxa, although we must remember that “*classification can only reflect existing knowledge and must be open to modification in the light of further discovery*” (Calman 1949, p. 21). The newly discovered high-definition fossil assemblage of the MUN Surface reveals important morphological and constructional data that guide our interpretation of the biology and palaeoecology of rangeomorphs and associated organisms. Our observations of specimens from the MUN Surface conform to the existing descriptive taxonomic scheme for rangeomorphs (Brasier *et al.* 2012), allowing us to resolve taxonomic problems within the Rangeomorpha, namely the *Beothukis/Culmofrons* dilemma. We suggest that the architectural approach used herein, whereby species are distinguished on the basis of continuous characters whereas genera differ in gross architecture or developmental program, can be extended with modification to aid taxonomic understanding of the Arboreomorpha/Frondomorpha. We also note that certain variables related to size and shape of organisms could be subject to the influences of taphonomy, ontogeny, or ecology, and should therefore only be used in taxonomic diagnoses with caution. Determining the extent of ecophenotypic variation in Ediacaran fossil assemblages may be a worthwhile avenue for future research. Other Ediacaran macrofossil taxa could similarly benefit from this consistent approach to taxonomy, allowing for the fact that higher-level classification of Ediacaran macrofossils is itself in a current state of flux. Consideration of the points outlined herein,

and critical appraisal of existing taxonomic schemes, will lead to an increasingly robust framework within which to reconstruct systematic relationships amongst the Ediacaran macrobiota.

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## AUTHOR CONTRIBUTIONS

AGL and JJM jointly discovered the site and conducted the field and laboratory studies. All authors were involved in data analysis and writing the manuscript.

## DATA ARCHIVING STATEMENT

Data for this study, including information on the sedimentology and stratigraphic setting of the MUN Surface, and six additional figures, are available in the [Dryad Digital Repository]: <http://dx.doi.org/10.5061/dryad.6r4j8>

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## EXPLANATION OF FIGURES AND TABLES

**FIG. 1.** Map and stratigraphic column (latter not to scale) showing the location of the MUN Surface. **A)** Newfoundland, Eastern Canada. **B)** The Avalon and Bonavista Peninsulas (see box in **A**), showing the major Ediacaran fossil localities of Mistaken Point, Spaniard's Bay, Ferryland, and the Catalina Dome. **C)** Geological map of the Catalina Dome (after Hofmann *et al.* 2008), showing major settlements, and the location of the MUN Surface (yellow star).

See the column for key to the geological units. Dates in the column are taken from Benus (1988) and Van Kranendonk *et al.* (2008, after Bowring *et al.* 2003), from correlative units on the Avalon Peninsula. Note that these dates have only been published in abstract form. Stratigraphy follows O'Brien and King (2005).

**FIG. 2.** Ediacaran macrofossils from the MUN Surface, Bonavista Peninsula, Newfoundland. **A)** Unipolar rangeomorph *Beothukis plumosa* comb. nov., preserved in negative epirelief. Note the clearly displayed second-order rangeomorph branches along the length of the frond. **B)** Silicon rubber cast (i.e. positive hyporelief) of a partial *Bradgatia* aff. *linfordensis* specimen. Primary branches are distally inflated, and can reach over 22 cm in length. **C)** Close-up image of *Bradgatia* from the MUN Surface preserved in negative epirelief, showing sub-mm resolution of preserved features. Scale bars = 10 mm.

**FIG. 3.** Ediacaran macrofossils on the MUN Surface, Bonavista Peninsula, Newfoundland. **A)** Juvenile *Primocandelabrum* sp., exhibiting clear first and second order branching. **B)** *Charniodiscus procerus*. **C)** *Fractofusus* sp. This specimen is too small to confidently identify to species level. **D)** *Charnia masoni*. **E)** Multiple superimposed macroscopic filaments, oriented in a variety of directions. Filaments vary from broadly straight to gently curving. Note the unweathered tuff still covering the surface at top left. A, B, D and E preserved in positive epirelief; C, preserved in negative epirelief. All scale bars = 10 mm except C) = 1 mm.

**FIG. 4.** A comparison of MUN Surface specimens with the type specimens of *Beothukis* and *Culmofrons*. **A)** Holotype specimen of *Beothukis mistakensis*, 'E' Surface, Mistaken Point Ecological Reserve, Newfoundland. **B)** Specimen from the MUN Surface, Burnt Point,



Bonavista Peninsula, Newfoundland. **C)** Holotype specimen of *Culmofrons plumosa* from the Lower Mistaken Point surface (cf. Clapham and Narbonne 2002), Mistaken Point Ecological Reserve, Newfoundland. **D)** Schematic diagram of a *Beothukis* frond, annotated to show the morphological features discussed herein. Images have not been retrodeformed, all fossil specimens remain in the field. Rangeomorph branches preserved as negative epirelief impressions. Scale bars = 50 mm, except B = 10 mm.

**TABLE 1.** Summary of the differences in characters used to diagnose *Beothukis* Brasier *et al.*, 2012, and *Culmofrons plumosa* Laflamme *et al.*, 2012. Characters in parentheses are added by us to assist comparison, and have been interpreted from the original diagnoses and descriptions. For those characters that are specified to differ between the two taxa (in italics), we state whether they are discrete or continuous, as discussed in the text. \*Note that in the original description of *Beothukis (mistakensis)*, Brasier and Antcliff 2009, neither a stem nor a holdfast disc was mentioned, though a holdfast was later recognized by Narbonne *et al.* (2009).